Originals

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Evolutionary Significance of the Variation of the Floral Structure of *Heloniopsis*

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The floral structures of the five species of *Heloniopsis* were compared. *Heloniopsis orientalis* (abbreviated as *O*) and *H. breviscapa* (*B*) have more advanced floral structures than *H. leucantha* (*L*), *H. umbellata* (*U*) and *H. kawanoi* (*K*). *O* and *B* are regarded as sister species sharing at least two autapomorphic floral characters (S-1 and S-2, designated in the text). The geographical ranges of *L, U* and *K* are south of those of *O* and *B*, without any overlap between the two groups. The range of species *B*, some of whose floral characters are more advanced than the other species, is south of its closest relative *O*, with some overlap of the ranges.

Heloniopsis is a small genus of Liliaceae comprising five species (Tanaka unpub.) distributed in eastern Asia (Krause 1930, Ohwi 1953, 1965, 1975). So far there has been little attempt to clarify the phylogenetic relationships among the species of this genus. In this study, floral structures of the five species were compared. Significant variations were found to exist in the floral structure of this genus. This paper focuses on these variations and presents their evolutionary and phylogenetic implications.

Materials and Methods

The following five species were investigated in this study; *H. leucantha* (Koidz.) Honda, *H. umbellata* Baker, *H. kawanoi* (Koidz.) Honda, *H. orientalis* (Thunb.) C. Tanaka, and *H. breviscapa* Maxim. Taxonomic circumscription for *H. breviscapa* in this paper coincides with Hara (1947). However, in this paper the infraspecific taxa of *H. breviscapa* designated by Hara (1947) are not adopted.

Floral structures were examined mostly in living plants listed in Table 1. These plants were cultivated at the experimental nurseries of Teikyo University in Hachiôji, Tokyo. The specimens in Table 1 are kept in our laboratory.

Geographical ranges of the species were determined in most cases by examining the herbarium specimens housed in MAK, RYU, TI and TNS.

Results

The name of each species is abbreviated as follows in the following description: *H. leucantha* = ***L***, *H. umbellata* = ***U***, *H. kawanoi* = ***K***, *H. orientalis* = ***O***, and *H. breviscapa* = ***B***.

In *O* and *B*, the base of each tepal is adnate to the base of its corresponding filament$^{1)}$, forming a sheath-like, saccate structure (designated here as **S-1**) (Figs. 1A–1C). During anthesis this structure is filled with nectar, secreted by the nectary at the bottom. In these

Table 1. Collection data of the materials. In this list, each entry includes in this order code (O-1, B-1,..), locality, date of collection (year, month/day), collector(s) and the other information. N.T. = N. Tanaka (the author of this paper)

H. orientalis

Honshu

- O-1: Niigata Pref., Santô-gun, Koshiji-chô, Hakama. 1987, 4/2. N.T. s.n.
- O-2: Niigata Pref., Karihane-gun, Oguni-machi, Mt. Hachikokusan. 1986, 4/6. N.T. s.n.
- O-3: Toyama Pref., Uozu-shi, Kosuganuma. 1983, 5/26. N.T. s.n.
- O-4: Nagano Pref., Kiso-gun, Nagiso-chô, Tadachi. 1981, 5/27. N.T. s.n.
- O-5: Gifu Pref., Motosu-gun, Neo-mura, Rav. Midoridani. 1987, 3/26. N.T. s.n.
- O-6: Aichi Pref., Inuyama-shi, Inuyama. 1987, 3/25. N.T. s.n.
- O-7: Shiga Pref., Shiga-gun, Shiga-chô, Mt. Hirasan. 1983, 5/28. N.T. s.n.
- O-8: Mie Pref., Mie-gun, Komono-machi, Yunoyama – Mt. Gozaisho; Yunoyama – eastern foot of Mt. Kirara-mine. 1981, 6/4; 1985, 5/22; 1987, 3/27–28. N.T. s.n.
- O-9: Wakayama Pref., Naka-gun, Mt. Ryûmon. 1981, 6/6. N.T. s.n.

H. breviscapa

Honshu

- B-1: Mie Pref., Taki-gun, Miyagawa-mura, Rav. Ôsugidani. 1984, 7/6–7. N.T. s.n.

Shikoku

- B-2: Tokushima Pref., Katsuura-gun, Kamikatsu-chô, Tanono. 1984, 6/5. N.T. s.n.

Kyushu

- B-3: Kumamoto Pref., Aso-gun, Kugino-mura,Yunotani. 1985, 6/2. N.T. s.n.
- B-4: Kagoshima Pref., Aira-gun, Makizono-chô, Myôken. 1985, 6/6. N.T. s.n.
- B-5: Kagoshima Pref., Satsuma-gun, Isl. Shimo-koshiki-jima, Mt. Odake. 1985, 6/3; 1988, 5/31. N.T. s.n.
- B-6: Kagoshima Pref., Tarumizu-shi, Mt. Takakumayama, along the upper stream of the Honjô River. 1983, 7/26. N.T. s.n.
- B-7: Kagoshima Pref., Kumage-gun, Isl. Yakushima. 1983, 7/28–29; 1986, 10/8. N.T. s.n.

H. leucantha

Ryukyu Isl.

- L-1: Okinawa Pref., Isl. Okinawa (-Hontô), Nago-shi, Genka. 1990, 8/11. Collected by the staff of the Research Inst. of Tropical Plant Resources in Okinawa s.n.
- L-2: Okinawa Pref., Ishigaki-shi, Isl. Ishigaki, along the upper stream of the Nagura River. 1984, 10/24. M. Yokota s.n.
- L-3: Okinawa Pref., Yaeyama-gun, Taketomi-chô, Isl. Iriomote, Mt. Komidake. 1990, 10/20. M. Yokota s.n.
- L-4: Okinawa Pref., Yaeyama-gun, Taketomi-chô, Isl. Iriomote, along the Urauchi River. 1987, 3/18. Collected originally by Yahara & Shimizu and then transplanted to the Bot. Gard. of the Univ. of Tokyo (accession number by this garden: 87–56)

H. umbellata

Taiwan

- U-1: Taipei Co., Mt. Chihsingshan. 1987, 10/15. N.T. s.n.
- U-2: Taipei Co., Mt. Tatunshan. 1987, 10/16. N.T. s.n.

H. kawanoi

Ryukyu Isl.

- K-1: Okinawa Pref., Ishigaki-shi, Isl. Ishigaki, Shiramizu (along the upper stream of the Nagura River). 1993, 7/30. N.T. s.n.
- K-2: Okinawa Pref., Ishigaki-shi, Isl. Ishigaki, Mt. Omoto, alt. 90 m. 1995, 3/2. Originally

collected by J. Murata, and then transplanted to the Bot. Gard. of the Univ. of Tokyo
K-3: Okinawa Pref., Yaeyama-gun, Taketomi-chô, Isl. Iriomotejima, along the middle and upper stream of the Urauchi River. 1983, 7/11. N.T. s.n.

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species, the neighbouring tepals are connate to each other at their bases, forming a low membraneous structure (designated here as **S-2**) between them (Figs. 1A–1C).

In *L*, *K* and *U*, on the contrary, there is no such distinct adnation between the tepal and the filament (Figs. 1D–1F) as that seen in *O* and *B*. The nectary in these three species is located, as it is in *O* and *B*, at the base of the ventral side of each tepal. However, the concave of the nectary is not sheath-like as in *O* and *B*, but shaped like a shallow bowl or basin in *L* (Fig. 1D) and *U* (Fig. 1F) and like a very shallow hollow in *K* (Fig. 1E). Further, in these three species, the neighbouring tepals are not distinctly connate at their bases (Figs. 1D–1F), although some very minor connations are observed often in *U* (Fig. 1F) and occasionally in *L* and *K*.

In *B*, the nectary is located generally higher in the relative floral position than it is in any other species (Fig. 2). That is, in *L*, *U* and *K*, the bottom of the nectary concave (designated here as **BN**) is located always lower against the upper surface of the receptacle or the lowermost position of the ovary (designated here as **SR**) (Figs. 2A, 2B). In *O*, BN is also usually below SR (Fig. 2C), but occasionally as high as SR. In *B*, on the contrary, BN is usually above SR (Fig. 2D), but occasionally as low as SR.

The basal, lowermost part of the dorsal side of each tepal is more or less convex in *L*, *U* (Fig. 3A), *K* and *O* (Fig. 3B) (this convex is termed the "**primary convex**" in this paper). For example, in *O*, this primary convex is relatively distinct, being slightly protuberant along the pedicel as shown in Fig. 3B, while that in *K* is very slight. This primary convex is consistently located just behind the nectary on the ventral side of each tepal in these species, and accordingly, the basal part of each tepal has more or less a concavo-convex structure. On the other hand, in *B*, there is some intraspecific variation on the character of the basal part of the tepal. For example, in the plants from Ôsugidani (B-1 in Table 1), the Kinki district of Honshu, central Japan, there is also a primary convex at the basal part of each tepal, which is morphologically similar to that of *O*. But, in the plants from Shikoku and Kyushu (B-2–B-7 in Table 1), western Japan, the primary convex is usually poorly or very scarcely developed(2) (Figs. 3C, 3D), and instead, the secondary, slight convex (this convex is termed the "**secondary convex**" here) is developed often at a site slightly above the lowermost part of the tepal (Figs. 3C, 3D). The presence of this secondary convex can also be traced occasionally even in plants from Ôsugidani, but it is usually so slight and indistinct(3) that it is likely to be overlooked. In *B*, as mentioned earlier, the nectary is located higher in the relative floral position than in any other species, and this character seems to be responsible for the development of the secondary convex in this species. In fact, it is observed that there is a good correlation between the position of the nectary and that of the secondary convex in this species. Detection of this secondary convex in *B* is usually easier in the flowers after anthesis (Fig. 3D) rather than in anthesis (Fig. 3C).

The geographical range of each species is as follows: *U*, Taiwan; *L* and *K*, the Ryukyu Islands; *B*, southwestern Japan (Kyushu, Shikoku and southwestern Honshu); *O*, Japan (the northern part of Kyushu, Shikoku, Honshu and Hokkaido), Korea and the southern part of Sakhalin.

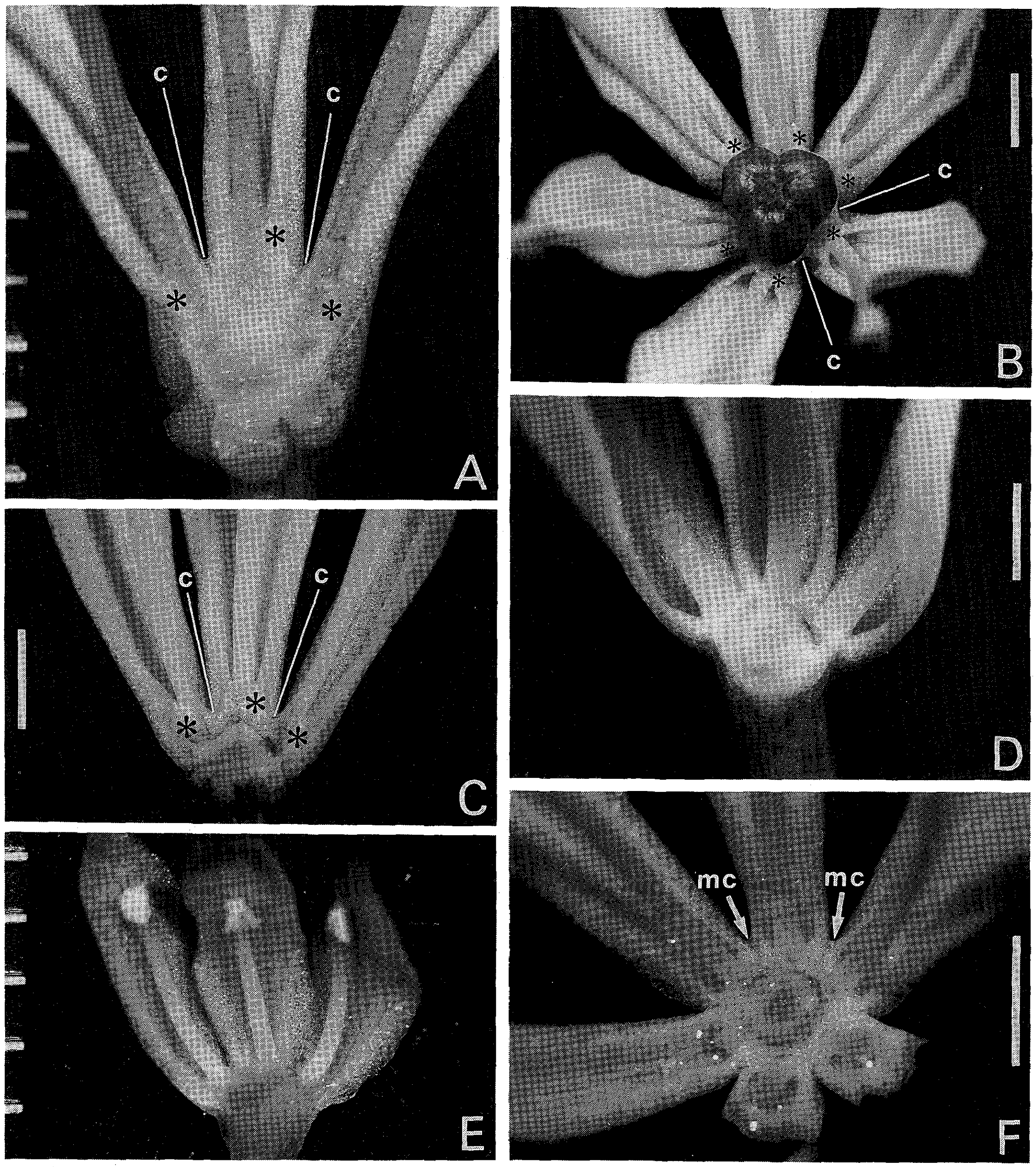

Fig. 1. Basal parts of flowers of *Heloniopsis*. Some floral parts are removed. A. *H. orientalis* (O-5). B, C. *H. breviscapa* (B-3). D. *H. leucantha* (L-1). E. *H. kawanoi* (K-1). F. *H. umbellata* (U-1). "c" in Figs. A–C shows the basal connation between the neighbouring tepals. "*" mark in Figs. A–C shows the adnation between the tepal and the filament. "mc" in Fig. F shows the very minor connation between tepals. In parentheses is indicated the code for each source of material (cf. Table 1). Scales in Figs. A and E are in mm, and the scale bars in the other figures indicate 2 mm.

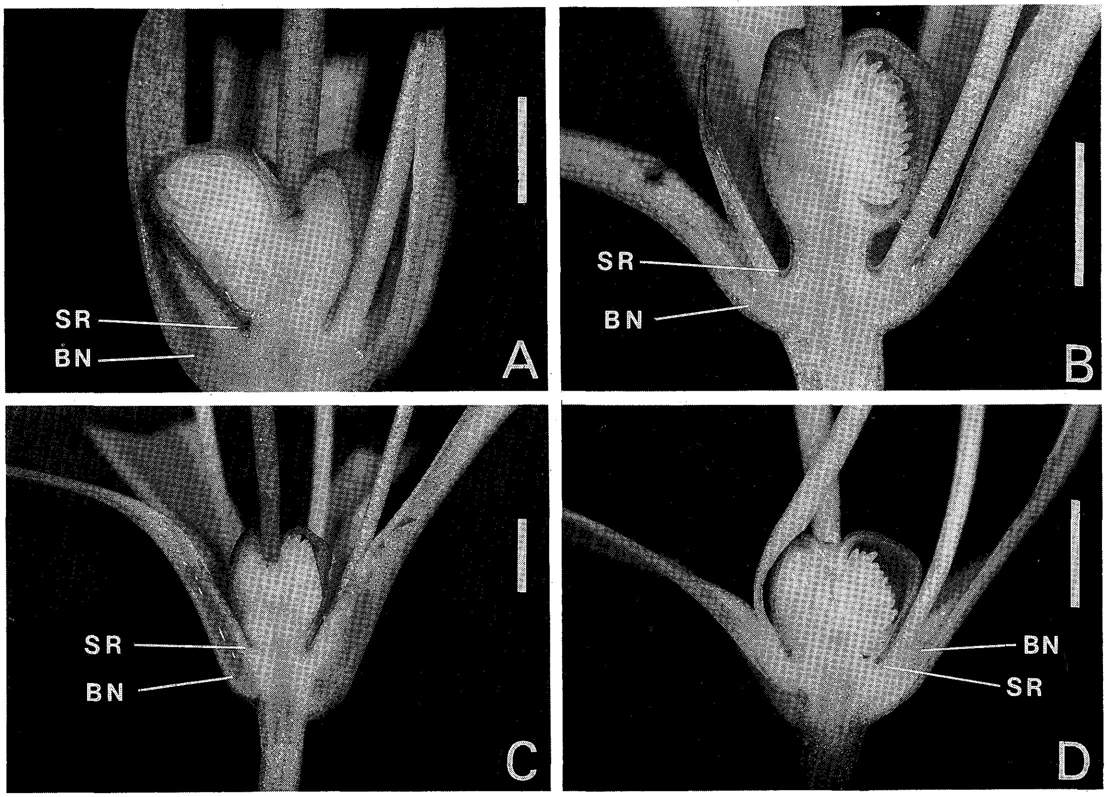

Fig. 2. Longitudinal sections of flowers of *Heloniopsis*. A. *H. leucantha* (L-1). B. *H. umbellata* (U-1). C. *H. orientalis* (O-5). D. *H. breviscapa* (B-7). "SR" indicates the upper surface of the receptacle (or the base of the ovary), while "BN" is the bottom of the nectary concave. Note that the position of the nectary in *H. breviscapa* (Fig. D) is higher than that in the other species (Figs. A–C). In parentheses is the code for each source of material (cf. Table 1). Scale bar = 2 mm.

Discussion

From an evolutionary point of view, a compound structure made up of subunit structures can generally be regarded as advanced or secondary compared with a non-compound, unit structure. This view seems also to be applicable to the case of *Heloniopsis*.

In the flowers of *O* and *B*, two such compound structures (S-1 and S-2) can be seen. One is the saccate structure (S-1) at the base of both a tepal and a filament. This structure is formed by adnation between the two different floral organs or units (a tepal and a filament). The other is the membraneous structure (S-2) connecting the bases of the neighbouring tepals. This structure is formed by connation between the same kind of floral organs or units (tepals). These two structures (S-1 and S-2) are regarded as advanced or secondary compared with structures that do not display adnation or connation. While these two structures (S-1 and S-2) are developed exactly in the same form in *O* and *B*, they are not appreciably developed in the flowers of *L*, *U* and *K*. These facts suggest that *L*, *U* and *K* are primitive with respect to the floral structure, while *O* and *B* are advanced. Further, *O* and *B* can also be regarded as sister species derived from a common ancestral lineage, because they share the above two autapomorphic floral characters (S-1 and S-2).

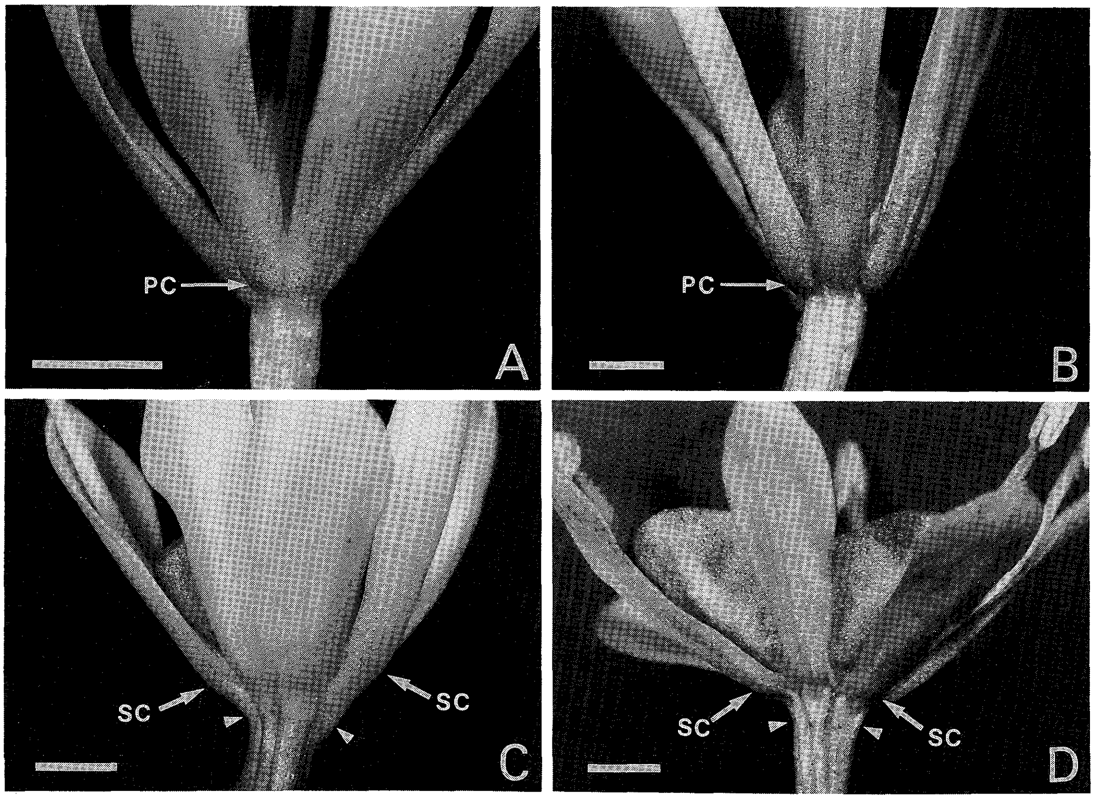

Fig. 3. Basal parts of tepals (the dorsal side) of *Heloniopsis*. A. *H. umbellata* (U-2). B. *H. orientalis* (O-6). C, D. *H. breviscapa* (B-2), C; in anthesis, D; after anthesis. In Figs. A and B, the lowermost part of each tepal has a primary convex (PC), while in Figs. C and D, the primary convex is scarcely developed (indicated by an arrowhead), and instead, the secondary convex (SC) is developed slightly just above the lowermost part. In parentheses is the code for each source of material (cf. Table 1). Scale bar = 2 mm.

The position of the nectary in the flowers of *B* is generally higher than that of any other species, as stated earlier. This character can also be regarded as advanced or apomorphic in state, since this character is developed only in *B*, which is one of the two sister species regarded to have more advanced floral structure than the other three species, as mentioned above. Probably, this character has developed in connection with the pollinators visiting the flowers of *B*. This character is not only a direct cause for the development of the secondary convex, but also likely to have been a trigger for the degeneration of the primary convex in some plants of *B*; in this species, the structural correlation existing primarily between the nectary and the primary convex is likely to have been weakened due to the transfer of the nectary from the lower position to the higher, and this altered condition seems likely to have induced the degeneration of the primary convex in some plants of *B*. As this degeneration of the primary convex is only seen in some plants of *B*, this character is also regarded as advanced or apomorphic in state. According to this interpretation, the plants showing this degeneration, like many plants from Shikoku and Kyushu, western Japan (B-2–7 in Table

1), are regarded as advanced with respect to the floral structure, and those without showing this degeneration, like the plants from Ôsugidani, the Kinki district of Honshu, Japan (B-1 in Table 1), are regarded as primitive, since the latter plants still retain the older character (the primary convex). The development of the secondary convex in B can also be regarded as an apomorphic character. In these respects, it can be said that *B* is the species having more advanced floral structure than its closest relative *O*.

There is no doubt that the evolution of the floral structure in *Heloniopsis* has proceeded in connection with its pollinators, because the major transformations found in the floral structure of this genus are more or less confined to the parts related to the nectary.

The ranges of the species with the most primitive floral structure (*L*, *U* and *K*) are south of those of the species with the more advanced floral structure (*O* and *B*), without any overlap between the two groups. The former group of species is distributed in Taiwan and the Ryukyu Islands, while the latter group in Kyushu to the north up to the southern part of Sakhalin. The range of species *B*, some of whose floral characters are more advanced than the other species studied here, is south of its closest relative *O*, with some overlap of the ranges.

The phylogenetic relationships among *L*, *U*, *K* and an ancestral lineage of both *O* and *B* are still not clear. Further comparative studies on many other characters of this genus are needed.

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Endnotes

[1] The presence of this character in this genus has been reported by Franchet (1887), and in *H. orientalis* by Uteck (1978) and Utech and Kawano (1981).

[2] The presence of this character has already been known mainly in the plants from Kyushu [Ohwi 1953, 1965, 1975; under the name of *H. orientalis* var. *breviscapa* (Maxim.) Ohwi. Kitamura et al. 1964, Kitamura and Murata 1966; under the name of *H. orientalis* subsp. *breviscapa* (Maxim.) Kitamura].

[3] The secondary convex could be distinguished only when the primary convex is poorly or scarcely developed. Some degree of the development of the primary convex may obscure in the external appearance the presence of the secondary convex, even if the latter is present.

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田中教之：**花部構造からみたショウジョウバカマ属の進化**

本属の5種について花部構造の比較観察を行った結果，種間もしくは種内で変異が見出された．*Heloniopsis orientalis*（*O*）と*H. breviscapa*（*B*）では，各花被片とそれに対生する各花糸がそれぞれ基部で合生し，鞘状の構造（内部の基底部には蜜腺がある）を形成している（この構造をS－1とする）．また，これらの種では，花被片内面の基部間で膜状の構造が顕著に発達している（この構造をS－2とする）．これらの構造（S－1とS－2）は，*H. leucantha* (*L*), *H. umbellata* (*U*), *H. kawanoi* (*K*)の3種ではほとんど発達していない（ごくわずかな程度での発達はとくに*U*などにおいてしばしば見られる）．これらの2構造（S－1とS－2）は進化の結果として発達した新たな（派生的な）構造であり，これらの構造を発達させていない構造は原始的な構造であると考えられる．*O*と*B*がこれらの2つの派生的構造をまったく同じように発達させていることは，両種が同一の祖先系統から派生した姉妹種であり，両種は花部構造的に見ると*L, U, K*よりも進化した種群であると見なすことができる．

*B*の花被片にある蜜槽の位置は同属の他種のそれと比べて概して少しより高い位置にある．*B*の花被片の外側最下部の膨らみ（これを一次的膨らみとする）には種内変異があり，膨らみが発達しない場合が多くある．また，*B*では花被片外側の最下部よりも少し上部にわずかながら二次的な膨らみが発達する場合がしばしば認められる．この二次的な膨らみの発達は，この種が蜜槽をより高い位置に持つためであり，また，この種において一次的な膨らみが発達しないことが多くあるのは，蜜槽がより高い位置にあることによって促された一種の退化現象によるものと見なされる．*B*に特異的に見出されるこれらの性質もしくは構造の発達も，進化的に見ると，新たに発達した性質（派生的性質）ないしは構造であると見なすことができる．*B*において，上記のような一次的膨らみをよく発達させていない個体群（九州や四国産にそのような個体が多い）は，それを発達させている個体群（本研究で用いた材料に限って言えば，三重県大杉谷産の個体群）よりも，花部構造の点においてより進化した（派生的な）群であると見なすことができよう．本属の花部構造の主だった変化は，主に蜜腺に関わる構造において起きていることから，その花部構造の進化には，この植物群の花を訪れるポリネイターが深く関わっていることは疑いない．

花部構造の観察結果に基づき，本属の種の分布域を概観すると，相対的にもっとも原始的な花部構造を持つ*L, U, K*の3種は台湾あるいは琉球に分布し，それよりも進化した花部構造を持つ*O*と*B*はそれよりも北部，すなわち，九州以北の日本，朝鮮（韓国・北朝鮮），サハリン南部に分布する．いくつかの固有な派生的花部形質を持つ*B*は，その姉妹種*O*よりも概して南部にその分布域を持っている（*B*の分布域：関東南部以西の本州西南部，四国，および九州）． （帝京大学文学部教育学科）